Ecuadendron (Fabaceae: Caesalpinioideae: Detarieae): A New Arborescent Genus from Western Ecuador

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ABSTRACT. A new genus and species of trees from mesic forests of lowland western Ecuador, *Ecuadendron acosta-solisianum*, is described. The new taxon is a canopy tree and is known from only three localities separated by a gap of 350 km. *Ecuadendron* is placed in the "*Brownea* group" of the tribe Detarieae (Fabaceae: Caesalpinioideae), and its closest relatives appear to include the monotypic *Brachycylix* from north-central Colombia, and *Heterostemon* and *Elizabetha* from the Guayana Shield area. With its long pendent inflorescences and particular suite of floral features, *Ecuadendron* appears to be adapted to pollination by bats.

The lowlands of western Ecuador, between the Andes Mountains and the Pacific Ocean, have become known as a region of high species richness and relatively high endemism for vascular plants (Dodson & Gentry, 1991). The region has been considered as one the world's most critical conservation "hotspots" for tropical forests, where high biological diversity and high rates of habitat destruction coincide (Myers, 1988).

Species-level endemism for vascular plants in the mesic forests of western Ecuador has been estimated at 20% of an estimated total flora of 5300 species (Neill, 1997). Endemism at the generic level has not yet been reported for western Ecuador, although some mesic-forest genera are shared only with the adjacent Chocó region of southwestern Colombia, and some dry-forest genera are shared only with adjacent northwestern Peru.

Recent botanical explorations in the mesic forests of western Ecuador have resulted in collections of a large canopy tree legume, which is described herein as a new genus and species in the tribe Detarieae (Fabaceae: Caesalpinioideae).

Ecuadendron acosta-solisianum D. A. Neill, gen. et sp. nov. TYPE: Ecuador. Azuay: Cantón Cuenca, Manta Real, at western base of Andes, 20 km SE of La Troncal, on lower slopes just above the village, primary forest remnant trees in cocoa plantation, Tropical Wet Forest life zone, 350 m, 02°34′S, 79°21′W, 7 Nov. 1995 (fl), *David Neill, H. Vargas, T. Núñez & J. Clark* 10437 (holotype, QCNE; isotypes, AAU, COL, GB, GUAY, K, NY, MEXU, MO, QCA, US).

Arbores Fabaceae Caesalpinioideae tribui Detarieis pertinentes. Folia paripinnata; petiolulis plicatis; foliolis bijugatis. Inflorescentia racemosa pendula; 2 m longa; bracteolis cupulatis. Flores resupinati; hypanthio cupulato; sepalis 4 cochleariformibus; petalis 5 clavatis, petalo inferiore ad basim incrassato; staminibus fertilibus 5 exsertis, staminodiis 4, filamentis ad basim connatis, hypanthio adnatis. Legumen pendulum lignosum velutinum; seminibus 4–9 oblongis vel quadrangulis.

Trees attaining 30 m, with dense oval crown; trunk to 50 cm DBH; bark light brown, mottled, peeling in flakes 1 cm diam., revealing darker blotches; slash reddish, with no detectable odor; wood dense and very hard; branchlets light brown, lenticellate. Stipules falcate-subulate, 5–8 mm long and 3 mm wide at base, irregularly caducous or often persistent, becoming somewhat lignified and covering the axillary bud, externally nerveless, minutely puberulent; leaves paripinnate, eglandular; petioles 7–15 mm long with basal pulvinus ca. 5 mm long, rachis 3–6 cm long, terete; petiolules 5–7 mm long, pulvinulate throughout their entire length and twisted or plicate (folded 180°), the leaflets thus disposed in a single plane but effectively resupinate; leaflets bijugate, chartaceous to thinly coriaceous, bicolorous, paler beneath, slightly arcuate, unequal in size, the margins entire; blade of basal pair 4–16 cm long, 2.7–7 cm wide, elliptic, inequilateral, the base acute with the upper margin meeting the costa at a point above the lower margin, apex bluntly acuminate, with 6–8 pairs of secondary veins; blade of distal pair somewhat more strongly arcuate and inequilateral than the basal pair, oblong to elliptic-oblong, widest near the apex, 13–25 cm long, 4–8 cm wide, base cuneate to acute, apex bluntly acuminate, with 11–14 pairs of secondary veins; costa and secondary veins slightly depressed above, strongly salient beneath. Inflorescence a pendent, axillary or ramuligerous, pedunculate raceme up to 2 m long; peduncle 25–60 cm long, the floriferous axis up to 1.6 m long with up to about 50 flowers arranged spirally, a single flower at each node but sometimes 2 or 3 nodes occurring close together on opposite sides of the axis; bracts absent; pedicels ca. 7 mm long; the 2 bracteoles 6–8 mm long, rounded at apex, almost

completely connate to form a broad cupular structure 7 mm wide. Flowers resupinate, such that the vexillar petal is held in the lowermost (adaxial) position; bracteoles, hypanthium, and calyx rose to brick-red; petals, androecium, and style ivory-colored; all floral parts glabrous except for velutinous ovary; hypanthium a broad thick-walled tube ca. 10 mm long; sepals 4, strongly imbricate in bud, 1.7 cm long, 1.5 cm wide at base, broadly rounded at apex, cochleariform; petals 5, clavate, 3.0–3.5 cm long, ca. 2 cm wide at widest point, broadly rounded at apex, the lowermost petal distinctly thickened at base with claw ca. 4 mm wide and 2 mm thick, the dorsal and lateral petals less strongly thickened at base; androecium of 5 fertile stamens alternating with 4 staminodes, these all connate at base into a cupular structure adnate to the hypanthium, free filaments of fertile stamens 3.0–3.2 cm long, ca. 2 mm thick, the anthers versatile, oval, ca. 10 mm long, ca. 3 mm wide, free filaments of staminodes 0.8–1.0 cm long, ca. 1 mm thick; pollen subspheroidal, tricolpate, ca. 35 μm diam., with coarsely verrucate ornamentation; gynoecium adnate to hypanthium at base, free portion 2.5–3.0 cm long; style 7–10 mm long, ovary 10 mm long, velutinous; gynophore 5–8 mm long, thickened at basal attachment to hypanthium. Pods pendulous from elongate peduncles, ligneous, 20–25 cm long, 4–5 cm wide, straight, the margins thickened, valve-faces ornamented with obliquely transverse ridges, rufescent-puberulous; seeds usually 4–9, compressed, oblong in outline or sometimes quadrangular due to pressure from adjacent seeds, 2–3.0 cm × 2.5–5.0 cm; testa thin, chartaceous, dark brown, when dry becoming brittle and separating easily from the cotyledons; aril and endosperm absent. Figures 1, 2.

Etymology. The generic name combines the name of the country of origin (Ecuador signifies "equator" in Spanish) with the Greek word for tree, *dendron*. The specific epithet commemorates Misael Acosta-Solís (1910–1994), Ecuadorian botanist and prolific writer, who carried out botanical inventories throughout Ecuador, promoted the science of botany and conservation of natural habitats, and published independently a number of works on the flora, vegetation, phytogeography, and useful plants of his native country.

Distribution and habitat. This species is known from only three localities in western Ecuador. The two southern populations are at about 2°30′S latitude: on the lower foothills of the Andes, just above the coastal plain, above the village of Manta Real in Azuay province (bordering on Cañar province; the exact provincial boundary is not clearly marked); and on the summit of Cerro Cimalón, an isolated hill to the west of the Andes near the Gulf of Guayaquil, within the Manglares-Churute Ecological Reserve in Guayas Province. At both these southern localities, *Ecuadendron acosta-solisianum* becomes a large canopy tree and is locally common within a very limited elevation range (about 300–350 m), but no more than about 50 trees are known to occur in each of the southern populations. The tree was first reported from Manta Real by R. Foster (in Parker & Carr, 1992) as a "possibly new species of *Browneopsis*." The northern locality, in Esmeraldas province on the western slopes of the coastal range (Cordillera de Mache), is at about 0°30′N, 350 km north of the two southern localities; the abundance of this species at the northern locality is unknown. All three sites are in wet to moist lowland tropical forest with considerable fog-associated precipitation. Most of the forests on the lower Andean foothills, and virtually all of the forests on the coastal plains in western Ecuador have been completely cleared for agricultural development during the past 50 years (Dodson & Gentry, 1991). It is possible, however, that additional populations of *Ecuadendron* are still extant in forest remants in the 350-km gap between the known southern and northern populations. Only the population within the Manglares-Churute Ecological Reserve has formal protection at present; forest clearing by farmers at the other two sites could exterminate those populations within a few years. At Manta Real the hard, dense wood is sometimes used in general construction, and the tree is known locally as "guabo jiche."

Phenology and pollination. Flowering specimens of *Ecuadendron acosta-solisianum* have been collected in the months of July, August, November, and December; at Manta Real the species flowered in July 1991 and 1993 but not in July 1995; in the latter year it flowered in November–December. There is, therefore, no clear-cut pattern of flowering phenology. Based on observations at Manta Real, fruits mature at about 5 months after flowering.

The long inflorescences pendent from stout branches, the gaping form of the flowers with exserted anthers, and the flower coloration, all strongly suggest that *Ecuadendron* is adapted to pollination by bats. The flowers are resupinate such that the vexillar petal is held in the lowermost (adaxial) position, and this petal is thickened and strengthened at the base; these features suggest that the adaxial petal may function as a landing platform for bats. The long pendent inflorescences and the form and position of the flowers, in fact, are reminiscent of those of *Kigelia africana* (Lamarck) Bentham (Bignoniaceae), the well-known and widely culti-

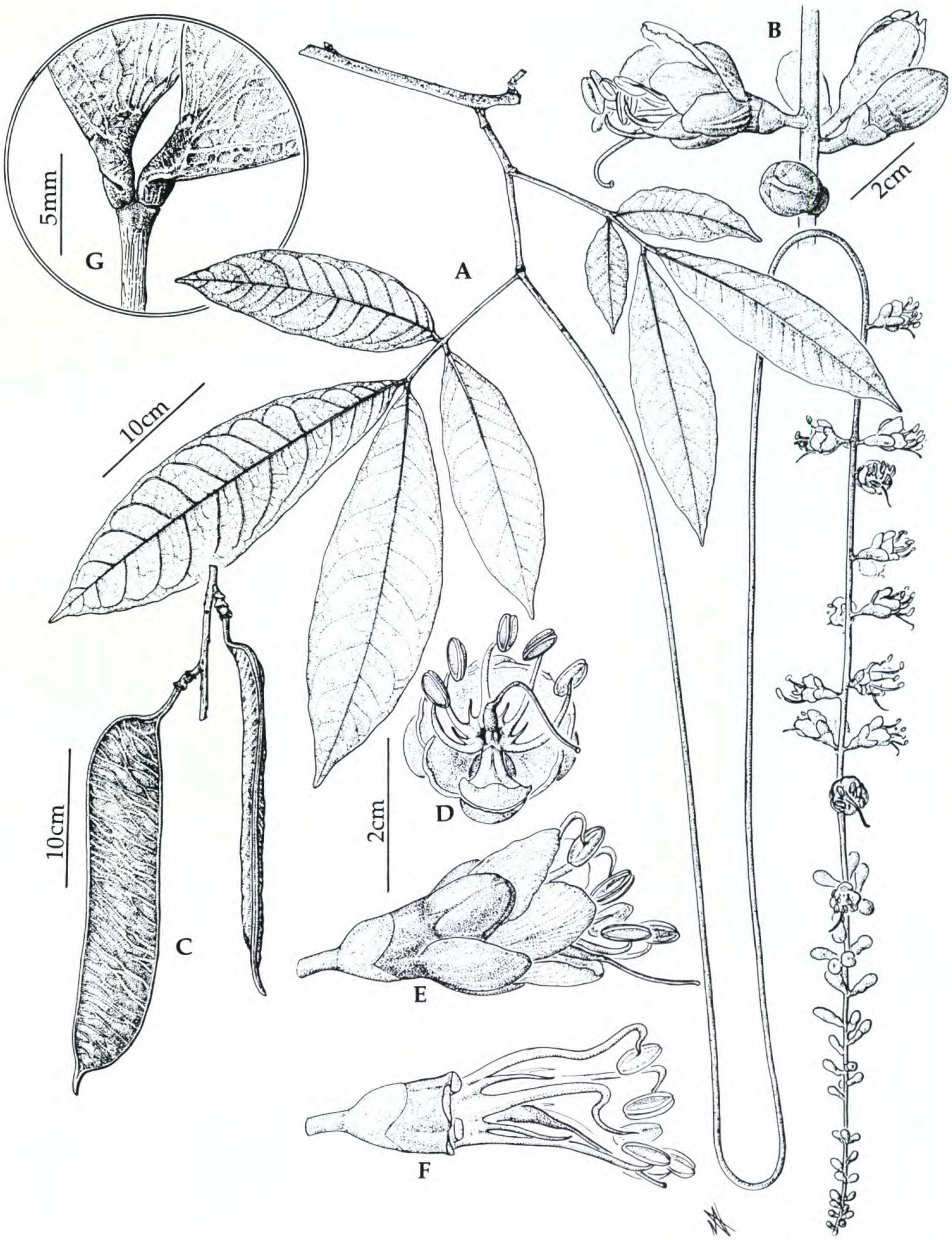

Figure 1. *Ecuadendron acosta-solisianum* D. A. Neill. —A. Flowering branch with pendent inflorescence. —B. Position of flowers on pendent inflorescence. —C. Pendent, mature fruits. —D. Open flower showing position of petals, androecium, and gynoecium. Note thickened base of lowermost petal. —E. Side view of open flower. At full anthesis, filaments are fully extended. —F. Flower with sepals and petals removed, showing position of androecium with fertile stamens and vestigial staminodes and gynoecium. Drawn from the type.

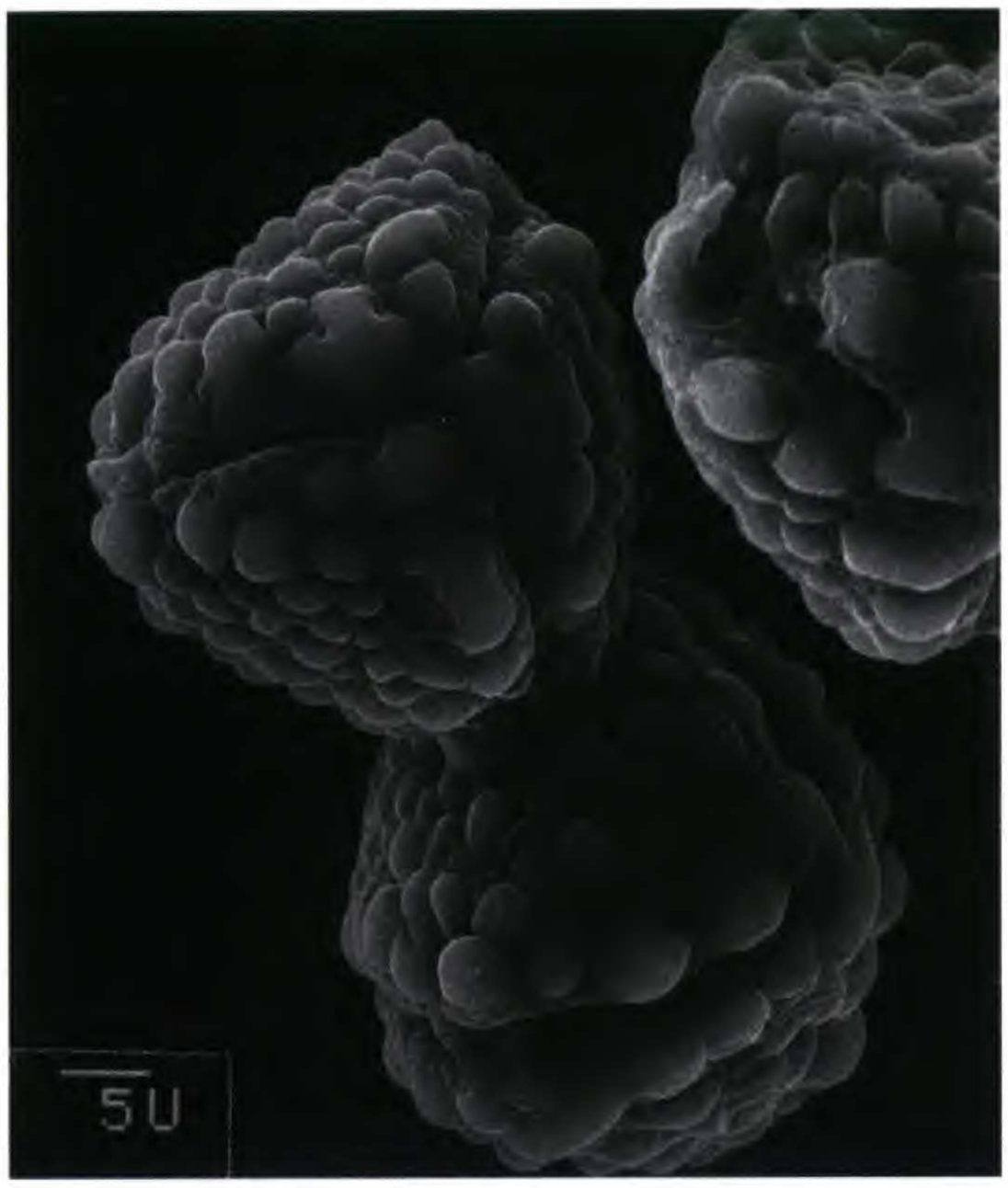

Figure 2. SEM image of pollen from the type of *Ecuadendron acosta-solisianum* showing tricolpate structure and coarsely verrucate surface ornamentation. Scale bar = 5 μm.

vated "sausage tree," which is a classic exemplar of chiropterophily (Faegri & van der Pijl, 1971). The coarsely verrucate pollen of *Ecuadendron* (Fig. 2) is simlar to that of several other bat-pollinated genera of Caesalpinioideae surveyed by Graham and Barker (1981), who suggested that such surface features of the pollen may be functional adaptations associated with bat-pollination. However, no nocturnal observations were made of *Ecuadendron* in flower, and visitations by bats have not been reported. A group of British students observed the hummingbird *Threnetes ruckeri* making repeated diurnal visits to the flowers of *Ecuadendron* at the Manglares-Churute population, but it was not clear that the hummingbirds were actually effecting pollination (Pople et al., 1997; Ian Burfield, pers. comm.). Flowers collected by the author at midday had no nectar and were odorless.

Relationships. This taxon clearly belongs in the tribe Detarieae DC. as circumscribed by Breteler (1995): the bracteoles are present and persistent after anthesis but do not cover the flower bud prior to anthesis, and the sepals are not reduced, such as occurs in the sister tribe Macrolobieae Breteler. Within the Detarieae, the relationships of *Ecuadendron* to other genera are not entirely clear. In Cowan and Polhill's (1981) key to genera of Detarieae, *Ecuadendron* would fall within the "*Brownea* group" by virtue of the fused bracteoles, and would key out next to *Brachycylix* (Harms) Cowan, with which it shares the 2-jugate leaflets, lack of bracts, cupular bracteolar structure, and 5 fertile stamens. *Brachycylix*, a monotypic genus with a restricted distribution in the Magdalena River valley of north-central Colombia, was originally described as a subgenus of *Heterostemon* Desfontaine. *Brachycylix* and *Ecuadendron* are both distinguished from *Heterostemon* by their petiolulate leaflets, pendent racemes, broad cupular fused bracteoles, and 5 rather than 3 fertile stamens. *Brachycylix*, however, has 3 petals while *Ecuadendron* has 5; moreover, the appearance of the androecium in the two genera is different. In *Brachycylix*, as well as in *Heterostemon*, the 9 staminal filaments are fused into a long inequilateral tube, open on one side; the central filaments are fused up to a higher point (about one-half their total length) than the outer filaments (cf. Cowan & Polhill, 1981: 129, fig. 4). In *Ecuadendron*, the staminal filaments form a much shorter, thicker, equilateral basal tube; the fertile filaments are of equal length and the alternating staminodes, much shorter and thinner than the fertile filaments, are also of equal length. In the structure of the androecium, with filaments fused basally into a short, thick ring, *Ecuadendron* more closely resembles *Elizabetha* Schomburgk ex Bentham than it does either *Brachcylix* or *Heterostemon*; *Elizabetha*, however, has only 3 fertile stamens, while *Ecuadendron* has 5, and differs from *Ecuadendron* also in the presence of well-developed bracts and a short non-pendent raceme.

The new taxon, in short, does not fit comfortably within any existing genus, but probably may best be grouped with *Brachycylix*, *Heterostemon*, and *Elizabetha*. In terms of geography, an interesting point is that *Heterostemon* and *Elizabetha* each contain several species and are essentially restricted to the Guayana Shield region, while *Brachycylix* and *Ecuadendron* are both monotypic, as far as known, and occur in restricted areas west of the Andes.

The twisted petilolules are a curious feature of *Ecuadendron*, which it shares with *Crudia* Schreber and some additional genera of Detarieae, but in *Ecuadendron* the petiolules are better described as plicate or "folded once and creased," while in *Crudia* they are merely twisted. The fruits and seeds of *Ecuadendron* bear a striking resemblance to those of *Brownea grandiceps* Jacquin and related species. This is not to suggest that the features shared between *Ecuadendron* and the latter two genera are synapomorphic, but rather to indicate the complex patterns of shared traits among the genera of Detarieae. A phylogenetic analysis of De-

tarieae, using molecular as well as morphological characters, would appear to be in order.

Paratypes. ECUADOR. **Azuay:** Cantón Cuenca, Manta Real, 350 m, 2°34′S, 79°21′W, 2 Mar. 1996 (fr), *David Neill, T. Núñez & A. Dik 10533* (collections from same tree as the type) (AAU, K, MO, NY, QCA, QCNE), 16 July 1991 (fl, fr), *Robin Foster 13587* (F, QCA), 23 Nov. 1992 (fl), *Karl Berg 102* (MO, QCNE), 29 Mar. 1993 (fr), *Karl Berg* 149 (MO, QCNE). **Esmeraldas:** Cantón Muisne, along Río Sucio between San Salvador community and Puerto Nuevo, 100–300 m, 0°30′N, 79°50′W, 1 Dec. 1995 (fl), *John Clark, Cyrus Brame & Manuel Marcia 1710* (MO, QCNE). **Guayas:** Cantón Naranjal, Reserva Ecológica Manglares-Churute, summit forest on Cerro Cimalón, 350 m, 2°26′S, 79°38′W, 9 Aug. 1996 (fl, fr), *D. Neill, T. Núñez & A. Dik 10648* (MO, QCNE).

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